ADDRESS

UPON THE

DEVELOPMENT OF THE BRAIN.

BY

WILHELM HIS,

PROFESSOR OF ANATOMY IN LEIPZIG.

Delivered in the Theatre of the Royal Dublin Society to the Follows of the
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MR. PRESIDENT AND GENTLEMEN,

It may be a little bold to deliver before you an English address, as I shall scarcely be able to express myself conveniently in your language. I must place all the responsibility on my dear friend, Mr. Cunningham; he has induced me to accept the honoured invitation of the Royal Academy of Medicine, and also to speak on the development of our brain, a theme which he could have treated himself as one of our best authorities.

It cannot be my task to enter into the high architectural complexities of the noblest of our organs; but, proceeding from embryological observation, I shall try to obtain some general points of view on the fundamental principles of its organisation.

Since the researches of C. E. v. Baer, and of R. Remak, we know that the nervous centres of vertebrates arise from the primary ectoderm as a canal of an epithelial character. It is also well-known that the brain-part of the neural canal forms, in the first instance, three enlargements—the fore-brain, the mid-brain, and the hind or rhombic brain. These three parts can be distinguished very early, even before the canal is closed. From the time of their first

formation they follow each other in a curve, or rather in a broken line. Owing to this curve the extremity of the brain canal is turned ventrally, and it extends beyond the extremity of the notochord and of the alimentary canal (Fig. 1).

FIG. 1.

Photographic reproduction of black-board drawing made by Prof. His for his Lecture.

    B. Diagrammatic representation of early condition of the neural tube, showing the manner in which it becomes bent on itself.

    A. Diagrammatic representation of a mesial longitudinal section through the head and neck of a human embryo. The brain-flexures and the optic vesicle are seen, and the manner in which the fore-brain is bent around the anterior extremity of the notochord and fore-gut is indicated. The early heart is shown bulging out in front of the foregut. The different sub-divisions of the brain are marked off from each other by dotted lines.

    In both diagrams (A as well as B) a dotted line running in the long axis of the neural tube indicates the separation of the alar from the basal lamina of the lateral wall.

The primary formation of the head is the same in all
craniote vertebrates. It shows a ventrally free, and a
fixed part—the fore-head and the back-head ; the latter
encloses the heart. The fore-head is formed by a frontal
and a facial piece. The frontal portion contains only the
fore-brain, while the facial piece includes the blind end of
the foregut and the extremity of the notochord. There
is a small field between the frontal and the facial pieces of
the head, where the base of the brain, the extremity of
the notochord, and the extremity of the foregut join
together. This field is of great morphological importance,
and it shows the place where the hypophysis is afterwards
to be formed. So long as the junction between the
foregut, the brain, and the notochord exists there is no room
for a hypophysis. But this junction is a temporary one,
and when it has been interrupted the ectodermal pouch of
the hypophysis enters into the gap.

The next advance in the development of the brain
brings about the separation of the eyeball from the fore-
brain, the division between the hemispherical and the
thalamic parts of it, and also the segmentation of the hind-
brain from the medulla oblongata. The boundary between
the two last-mentioned parts is marked by a flexure called
the pontine flexure (Fig. 6, p. 11 ; Fig. 14, Pl. II.).

Before following further changes, I have to say some
words about the histological development of the neural
canal. The wall of the neural canal shows already, before
it is closed, two different kinds of elements—(1) cells
extending through the whole thickness of the wall, and
forming a columnar epithelium ; and (2) round germinal
cells placed on its inner side.

The columnar epithelium undergoes a special transforma-
tion. Between the inner parts of its cells arises a regular
succession of open clefts whilst the tops of the single

eolumns remain united by a fine limiting membrane. The peripheral parts of the cells form a sponge-like network with irregular meshes. The whole formation is ealled the myelosponge, and its elements are termed the spongioblasts (Plate I., Fig. 10 and Fig. 11).

The round germinal cells are dispersed through the clefts of the internal colnmnar part of the myelosponge. Many of these cells are in full process of multiplication, and show the different stages of karyokinesis. Others grow out in the form of pear-shaped corpuscles (Plate I., Figs. 10 and 11; Plate II., Fig. 12). Each of these sends out a tapering protoplasmic prolongation, directed outwards towards the surface of the medulla. These pear-shaped corpuscles are the neuroblasts, and their prolongations constitute the origin of nerve-fibres. The formation of neuroblasts is confined to the two thiek lateral walls of the neural eanal. The roof and the floor of the tube are thinner than the side-walls, and they furnish only epithelial eells, or spongioblasts.

The primary neuroblasts have merely neural proeesses: the dendrites or ramified processes arise later than the nerves, and it seems that these attain very slowly their full development. A certain number of the newly-formed nerves leave the neural eanal to reach muscles, whilst others remain in the thickness of its wall. We find therefore motor fibres and internal or intra-medullary fibres. The motor fibres all come from the ventral half of the canal; the internal fibres start partly from its dorsal, partly from its ventral half. Some of them are commissnral fibres, and cross the mid-line; others enter into the longitudinal columns of the medulla.

All sensory nerves, also the fibres of the olfactory, the optic, and the auditory nerves arise outside the neural canal. The sensory nerves spring from the bipolar cells of

the spinal ganglia; the fibres of the olfactory nerve from
the epithelial cells of the olfactory groove, and the true
optic fibres from the neuroblasts of the retina. All these
nerves reaching the neural canal from without apply
themselves to its surface, and form longitudinal bundles.
The dorsal column of the spinal cord, the spinal roots of
the trifacial nerves, the auditory and the optic nerves are
all in their first appearance in loose connection with the
neural canal.
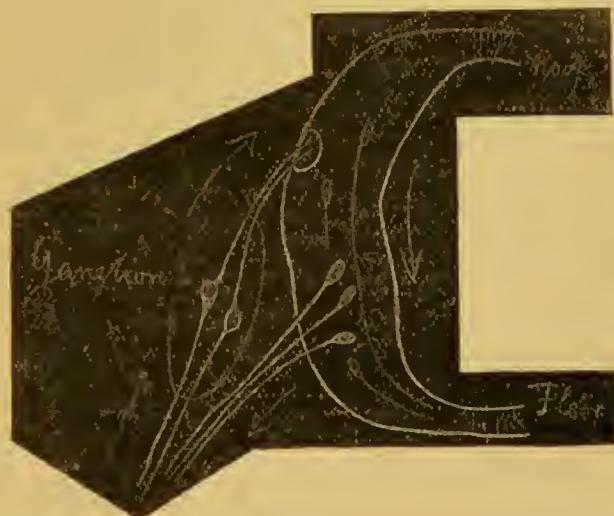
Fig. 2.

Photographic reproduction of a black-board drawing made by Prof. His
for his Lecture.

It gives a diagrammatic representation of a transverse section through
the spinal portion of the early neural tube. It is sufficiently
described in the text.

A section through the brain or the spinal cord of a
human embryo of about four weeks gives the plainest
representation of the typical architecture of nervous centres.
We find the motor fibres starting from the ventral half of
the canal (Plate III., Fig. 16), the sensory fibres reaching
the surface of its dorsal half, and internal fibres forming
connecting arches (Fig. 2). These three kinds of fibres
represent the groundwork of all central organisation: they

supply the paths from the periphery to the centre, those
from the centre to the periphery, and the paths from one
part of the centre to another. Every fibre coming from
a single cell forms with its cell a histological and physio-
logical unit, which we now call a *neuron*.

I return to the history of the brain. The most striking
feature in its morphological development is the general
increase of its flexures; that increase shows many varia-
tions in the different classes and orders of vertebrates.
Generally the two limiting flexures of the mid-brain pre-
cede the others in their progression. The base of the
fore-brain is brought near to that of the hind-brain. A
narrow cleft between these two parts leaves the place
for the dorsum sellæ (Fig. 6, p. 11; Plate II., Fig. 14);
this cleft persists even in the adult brain. By the new
nomenclature it is called the interpeduncular groove, and
it shows an anterior and a posterior recess, corresponding
to the two primary limits of the mid-brain.

The flexures of the rhombic brain follow a little later in
their development. The pontine flexure at the superior,
and the neck-flexure at the inferior end of the medulla
oblongata become very considerable, and the neural canal
assumes thenceforth a zigzag-like conformation (Plate V.,
Fig. 25). There is also a constant but feeble flexure in
the isthmus or narrow part of the rhombic brain. At the
same time the neural canal loses its primary simplicity.
Its parts begin to acquire more characteristic forms, and
we can soon distinguish all the principal parts of the
developed brain.

Before entering into any details it will be necessary to
follow the transformation of the primary longitudinal
laminæ. If we leave aside the purely epithelial or epen-
dymal laminæ of the neural canal, its roof and its floor, we
find its wall consisting of a ventral or basal, and of a
dorsal or alar lamina. As we have already seen the basal

lamina contains the motor centres, whilst the dorsal lamina receives the sensory nerves. The boundary-line between these two laminæ of the wall is generally well marked in the brain canal; its terminal end can be followed through

FIG. 3.

Photographic reproduction of a black-board drawing made by Prof. His for his Lecture.

It gives a diagrammatic representation of a transverse section through the rhombic or hind-brain (medulla oblongata), and is specially intended to show the alar and basal longitudinal laminæ of the lateral wall of the tube. Into the alar lamina the sensory fibres from the cells of the ganglion of the tenth nerve (vagus) are entering, so as to form a longitudinal column of fibres cut transversely and lying close to the surface. This is the "solitary tract" which later becomes deeply buried within the substance of the medulla. The neuroblasts of the nuclei of origin of the twelfth (hypoglossal) and of the eleventh or spinal accessory nerves are seen sending their motor fibres out from the medulla.

[In this drawing Professor His makes use of the English word " zone," and he thus follows his distinguished American friend, Professor C. S. Minot, of Boston. (See Minot's " Human Embryology," p. 606). But " zone " is altogether an inappropriate word to apply to either of the two

the third ventricle to the optic stalk, or optic recess. The further development of these two laminæ is disproportionate in the different parts of the brain. In man and in the higher vertebrates the basal lamina diminishes as we ascend from the lower to the higher parts; the motor centres begin to be discontinuous and to fail, and the last of them—the oculomotor centre—belongs to the mid-brain. The basal lamina of the fore-brain has no motor centres and is very reduced. It contains the mammillary body and the infundibulum, and is separated from the thalamus by a shallow furrow. We call it now the hypothalamus.

The alar lamina of the brain canal remains feeble in the medulla oblongata, but its growth is mighty in the higher parts, and results in the development of the cerebellum and of the cerebral hemispheres. In lower vertebrates the basal or hypothalamic lamina of the fore-brain is of more importance than in the higher ones, whilst the alar or hemispheric part remains less developed.

In the rhombic brain the alar lamina furnishes the restiform and the olivary bodies, the cerebellum and the superior peduncles, whilst the basal lamina gives the floor of the fourth ventricle. In the embryo of four weeks the rhombic brain when seen in transverse section has a pentagonal form, the epithelial roof being broad and the basal and alar laminæ forming together an obtuse angle. The motor centres lie near to the surface of the basal laminæ, and their fibres leave the canal wall

portions of the neural tube in question. The term "zone" could only be properly given to an area or strip of the neural wall which is placed at right angles to the long axis of the tube and which extends, girdle-like, around its circumference. The districts referred to, however, so far from presenting this relation, run parallel to the long axis of the tube. Still further, by using the word "zone" we do not give a correct translation of the German term (*Platte*) employed by Professor His himself. *Flügel-platte* (alar lamina) and *Grundplatte* (basal lamina) are the names used by Professor His to designate the two thick portions of each lateral wall of the neural canal. In the text the term "zone" has been changed to "lamina."]

in two lines—a mesial one and a lateral. Near the lateral motor line is the place where the sensory fibres come from without to the surface of the medulla, to form longitudinal bundles of fibres. As typical instances we can cite the two motor lines of the hypoglossal and the spinal accessory nerves, and close by the sensory roots of the pneumogastric nerves (Fig. 3). The longitudinal bundle receiving the sensory fibres of pneumogastric and of glossopharyngeal nerves is called the solitary tract; its primary position is very superficial. In the fully
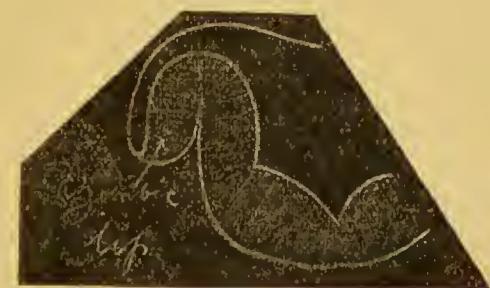
FIG. 4.

Photographic reproduction of a black-board drawing by Prof. His to explain the folding over of the rhombic lip of the rhombic or hind-brain in the region of the fourth ventricle. It represents a diagram-matic transverse section through the medulla oblongata.

developed medulla the solitary tract, and also the nuclei of the hypoglossal and accessory nerves, are separated from the ventral surface by a broad layer of tissue containing nerve-cells and also nerve-fibres running in all directions. How is this layer formed? The dorsal border of the alar lamina stands straight and erect during its primary stages, but it afterwards begins to bend outwards in the form of a longitudinal fold, which projects in a lip-like way along the entire length of the rhombic brain (Fig. 4). This rhombic lip (Rautenlippe) is the origin of the cerebellum and of the olivary bodies. (Plate II., Fig. 13.)

The formation of the cerebellum is not very difficult to

understand, but that of the olivary bodies presents a
greater amount of complexity, and is one of the most
interesting processes in the history of the brain. The
rhombic lip becomes adherent to the remaining part of the
alar lamina, and sends out a multitude of neuroblasts which
wander towards the middle line and pass on the ventral
side of the basal lamina, superficial to the solitary tract,
and the motor nuclei. These neuroblasts and their arched
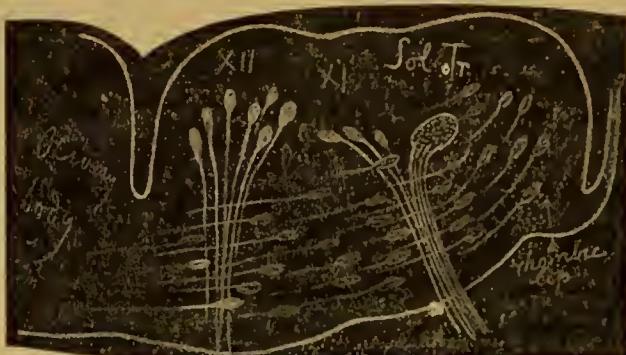
FIG. 5.

Photographic reproduction of a black-board drawing by Prof. His to
show the migration of neuroblasts from the region of the rhombic
lip—a developmental process by means of which the solitary tract
becomes deeply buried within the substance of the medulla. This
figure represents a later stage of the medulla than that depicted in
Fig. 3, and, as in the latter, it shows the neuroblasts which give
origin to the motor fibres of the hypoglossal and spinal accessory
nerves.

fibres are supported by the outgrowing myelosponge of
the basal lamina, and they form a thick layer containing
together with other nuclei those of the olivary bodies.
Afterwards longitudinal fibres of different origins and new
arch-like fibres join them to produce the final organisation.

The medulla gives a good example of the relation
between the local and the chronological succession of the
layers of the brain. The oldest layer of the medulla is the
floor of the fourth ventricle, with its nuclei. It is followed

in the first instance by the reticular formation, and afterwards by the layer containing the olivaries and other nuclei. Last of all come the pyramids and the outer arcuate fibres (Fig. 6A).

In the pons Varolii similar relations between the chronological and local succession of layers are to be established. For instance, we can cite the primitive position of the

Fig. 6.

Figure obtained of the head and neck of a human embryo of five weeks from a series of consecutive sections by the reconstruction method. It exhibits the different sub-divisions of the brain at this period, and shows particularly well the thalamic brain with the early outgrowth from it which ultimately forms the cerebral hemisphere.

motor nuclei of the trifacial nerve and of its spinal sensory root, and compare it with the later position, which shows these parts covered by thick layers of transverse and longitudinal fibres. In the mid-brain the tegmental part is the first formed. It presents itself as a thick prominence of the basal canal wall. In this prominence we early distinguish the nucleus of the oculomotor nerve and the posterior longitudinal bundle; then comes also a reticular formation, followed by the substantia nigra. The fibres of the crusta are partly very late formations.

I beg leave to limit my remarks concerning the thalamic
brain to the demonstration of photographs, and to pass
immediately to the primitive history of the cerebral hemi-
spheres.   The cerebral hemispheres are formed by the
terminal piece of the alar brain lamina, and this place can
be determined very early as an angular field situated
between the optic vesicle, the terminal, and the dorsal
border of the neural canal (Fig. 1, p. 2).   This field has
two free borders and one fixed; the free borders being the
terminal and the dorsal ones, the fixed border remaining
in continuity with the thalamic brain and with the stalk of
the optic vesicle.
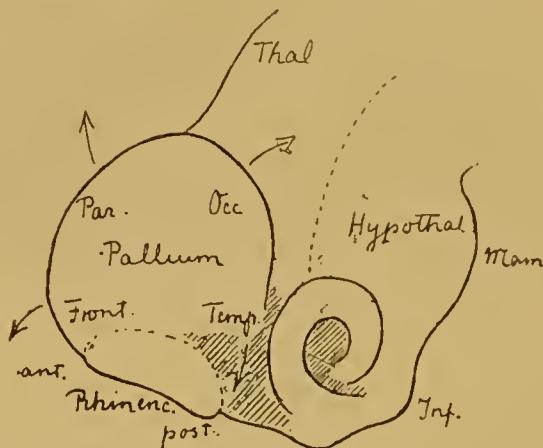
FIG. 6A.

The primary hemispheric brain is undivided.   The
separation of two hemipheres by a longitudinal fissure
begins in the human embryo at the end of the first month.
From this time we distinguish also the place of the nasal
brain or rhinencephalon of Sir W. Turner (Fig. 6A).   The
rhinic brain is situated immediately beneath the terminal
border of the brain tube.   Between its two halves appears
the thin lamina cinerea.   It represents the terminal section
of the alar brain lamina; the suture of the basal lamina is
enclosed in the optic chiasma and in the anterior wall of
the infundibulum.

The nasal brain is limited by Sir William Turner's rhinic fissure, and it is divided by another fissure, the fissura prima, into an anterior and a posterior part. The anterior part furnishes the olfactory bulb, tract, and trigone, and the field of Broca (area Brocæ). The posterior part remains as the wall of the anterior perforated space, and as the gyrus subcallosus (peduncle of the callosum). In the developed brain the anterior part of the rhinencephalon is fixed to the frontal lobe, the posterior part to the temporal lobe; these relations will enable us to distinguish from the earliest times the position of the hemispheric lobes. It is easy to see that the frontal lobe is directed partly towards the anterior, partly towards the dorsal border of the hemispheres. The temporal lobe is represented by the inferior part of the fixed border, the occipital lobe by its superior part, and the parietal lobe by the posterior part of the dorsal border (Fig. 6A).

The rhinic fissures and the fissura prima are folds of the brain-wall—and on its internal side they form three prominences, the first traces of a striate body. This part of the brain-wall increases very quickly, and forms the well-known prominence in the floor of the lateral ventricle. During many months the striate body shows its three branches, and remains in close relation to the lobes of the nasal brain.

The problem of brain formation has its histological as well as its morphological side, and we have to consider both. To a large extent the changes in the form of the brain depend upon the increase of its histological elements; but the increase of these elements is again ruled by the form of the surrounding parts, inasmuch as cells and nerves need free room to extend themselves.

To understand the complicated interlacement of the different processes, it is necessary to follow their chronological succession. Time is the mightiest factor in every

development. As we have seen before, the local position
of the layers of the brain depends on it; but it possesses
far, even much more, influence on the physiological
organisation of the neural system. Some examples may
explain this:—In the spinal cord, the myelosponge is the
first formed part of the tissues, its inner clefts furnishing
the room for the germinal cells and for the neuroblasts.
The meshes of the outer network are only pervious to
nerve-fibres, but not to nerve-cells. On this account
the different density of the myelosponge in its inner and
outer layers determines the separation of the grey and white
matter of the spinal cord. In the brain things seem to be
more complicated. We find there evident cell-emigrations
from the inner to the outer side of the canal wall.

The formation of nerves begins with the motor fibres;
the sensory fibres follow soon afterwards. These two
kinds of fibres are not only formed very early, but this
formation is also soon brought to an end. All the later
generations of neuroblasts furnish only internal connecting
fibres. The cells are formed during the first two or three
months of the embryonic life, but the fibres going out
from them can grow indefinitely long, before they reach
their destination. Also the dendritic or ramified processes
of central nerve-cells and the collateral fibres grow very
slowly, and we can scarcely say how long their formation
and their increase can continue. The regeneration of
sectioned nerves shows that even during later life nerves
can continue to grow.

In the whole neural canal, especially in the brain, the alar
lamina is slower in its development than the basal lamina.
But as it grows continually through long periods of time
enormous organs like the cerebral hemispheres may be
produced. In every case the new formation of neural
elements must necessarily be a process of superaddition.
The cells and the nerve-fibres once formed persist: they

are joined by other cells and fibres formed afterwards.
The older and the younger cell formations become con-
nected together; and, by the succession of different genera-
tions, the whole system will become more and more
complicated. In all these things time will multiply the
most intimate connections between the different parts.
The medulla oblongata is the first formed of the brain
parts. All the later formed parts enter into connection
with it, and finally it is the most central and most com-
plicated of all these parts. We may, therefore, make the
generalisation, that during the earlier periods of develop-
ment the single elements of the neural system in their
rough connections are formed, and that only during the
later developments the intimate organisation of the whole
system and the dependence of all its parts upon each other
is established.

All the higher functions of our brain depend upon the
anatomical and physiological superposition of neural
centres. By physiologists such superpositions have been
presumed many years ago, but only the inquiries of
recent times have given full evidence of their anatomical
disposition. The iron methods of Weigert, the silver
methods of Golgi and of Cajal, and the methyline blue
methods of Ehrlig have armed anatomical workers with
strong weapons. We can now trace the nerve-fibres from
their beginning to their final terminations; we can distin-
guish the fibres entering into a neural centre from the
fibres issuing from it. The rich and very unexpected
system of collateral fibres has been uncovered before our
eyes—a system which enables a single fibre to enter into
relations with long series of terminal points. By the new
anatomical methods applied to the undeveloped brain
Flechsig and Held could, for instance, follow the auditory
paths from their first origin in the cochlear ganglion to the

nuclei of the medulla oblongata. From thence new paths
are established to the upper olivary bodies, and to the
lower quadrigeminal body, and at last come the paths
from these centres of the mid-brain to the cerebral cortex
of the temporal lobe. There are at least four different cell
stations, every one being a centre with many particular
connections, and all united together in a harmoniously
working apparatus.

But the brightest victory of anatomical methods is the
analysis of the cerebral cortex given in these last years by
Prof. Flechsig. The controversies concerning the localisa-
tion or non-localisation of cerebral functions are not new.
Gall on the one side, Flourens on the other, were in
former periods the champions of the two parties. Since
that time the physiological inquiries of Hitzig, Ferrier,
Horsley, Schäfer, and many others, have given the decision
for the localisation, and the experiments of Mr. Horsley
have taught us how precisely the centres of different
muscles can be isolated in the cortex. Prof. Flechsig on
his side pursuing, for more than twenty years, by anatomical
methods the course of central nerve-bundles, has at last
succeeded in limiting in a sharp way the different special
sensory centres of the cortex—the centres of the optic, the
auditory, the olfactory nerves, and those of the nerves of
general sensibility. Each of these centres has its own
particular field on the brain surface—the optic centre in the
occipital, the auditory centre in the temporal, the olfactory
centre in the frontal lobe, while the centres of general sensi-
bility are situated partly in the frontal and partly in the
parietal lobe. All the centres receive projection fibres from
the internal capsule. They are separated one from the other
by large fields of cortex, which are without any connection
with projection fibres. The sensory cortex-centres show
medullated fibres from the time of birth, or soon afterwards.

In the rest of the cortex the medullated fibres appear later, and they develop from the side of adjacent sensory centres. These parts of the cortex are regarded by Prof. Flechsig as centres of association, and it may be remarked that of the two principal centres of association the parietal one is placed between the optic, the auditory, and the tactile centres, whilst the other, the frontal one, has only few direct connections with the sensory centres.

I cannot go farther in following the consequences of these new discoveries, but I think that we anatomists feel profoundly satisfied by the fact that discoveries of such general importance can be made by our science. We rejoice not only in what we know, but even much more in the perspective of coming knowledge. Anatomy is not a closed science, as it was asserted some time ago. It is a science full of life, and one of the most promising branches of general biology.

EXPLANATION OF PLATES.

The figures in the following five plates are reproductions of some of the more important lantern slides which were shown by Professor His during his Lecture. Figures 7-17 (Plates I.-III.) are photographs from the original preparations. Figures 20-27 are photographs from wax models:—

PLATE I.

Fig. 7.—Mesial longitudinal section through the neural tube of an early chick embryo. The aperture or neuroporo (*n.p.*) at the anterior end of the tube is still open.

Fig. 8.—Mesial longitudinal section through the head-end of a slightly older chick embryo, showing the intimate connection between the anterior end of the notochord (*n.*) and the hinder part of the floor of the fore-brain. Note that the neuropore is closed.

Fig. 9.—Early embryo of a dog-fish. The upper end of the figure shows the enlargement and bending of the brain-part of the neural tube.

Fig. 10.—Microphotograph of a portion of a transverse section through the neural tube. The inner ends of the spongioblastic columns are observed to be flattened out and joined together to form a fine limiting membrane. This is seen in the upper part of the section. Between them three germinal cells, two on the left with karyokinetic formations, may be seen.—Human embryo of four weeks.

Fig. 11.—In this microphotograph the neuroblastic cells are dark-coloured, and in connection with many of these the tapering axis-cylinder processes are seen. It will be observed that these processes are growing towards the surface (*i.e.*, the lower part of the figure) through the mesh-work of the myelosponge.—Human embryo of four weeks.

PLATE II.

Fig. 12.—Microphotograph of a portion of a transverse section through the whole thickness of the neural tube. The arrangement of the neuroblasts and of the spongioblasts is well seen. The limiting membrane on the inner aspect of the tube is uppermost in the figure.—Human embryo of four weeks.

Fig. 13.—Transverse section through the early medulla showing the rhombic lip.

    r.l.—Rhombic lip.   *G.x.*—Ganglion of the vagus.

Fig. 14.—Mesial section through the head of a human embryo of the seventh week. It shows the great expansion of the cavity of the brain-part of the neural tube as well as the strongly-marked brain flexures.

Fig. 15.—Photograph of a human embryo of six weeks. The different subdivisions of the brain shining through the thin head-coverings are well seen, and the cervical, pontine and mid-brain flexures observed, in section, in Fig. 14, are prominently brought out. Compare with Fig. 6 in the text (page 11).

PLATE III.

Fig. 16.—Transverse section through the spinal part of the neural tube of a human embryo of four weeks. It shows the early condition of the roots of a spinal nerve. A diagrammatic representation of this is given in Fig. 2 in the text (p. 5).

    c.c.   Central canal of neural tube.

    m.r.   Motor fibres from the neuroblasts in the wall of the tube, growing out to form the anterior nerve-root.

    S.G.   Spinal ganglion, from the cells of which the fibres grow into the wall of the neural tube and thus form the posterior nerve-root.

Fig. 17.—Section through a portion of the wall of the brain tube at the level of the origin of the fifth cranial nerve. It has been found necessary to turn this figure round on its side so as to make it fit into the plate.

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n.

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r. l.

G. X.

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PLATE IV.
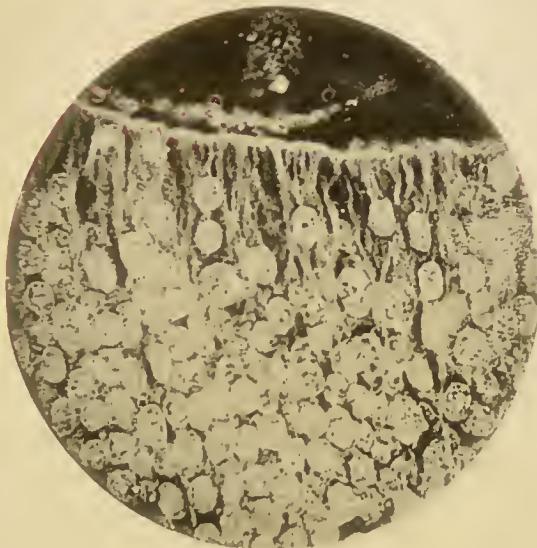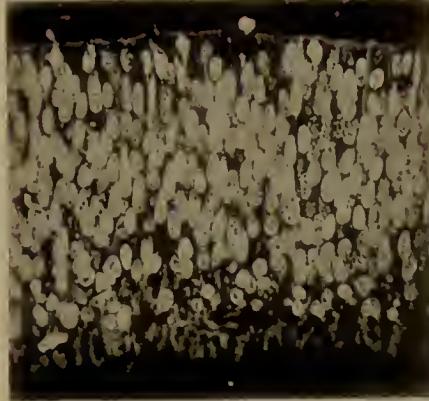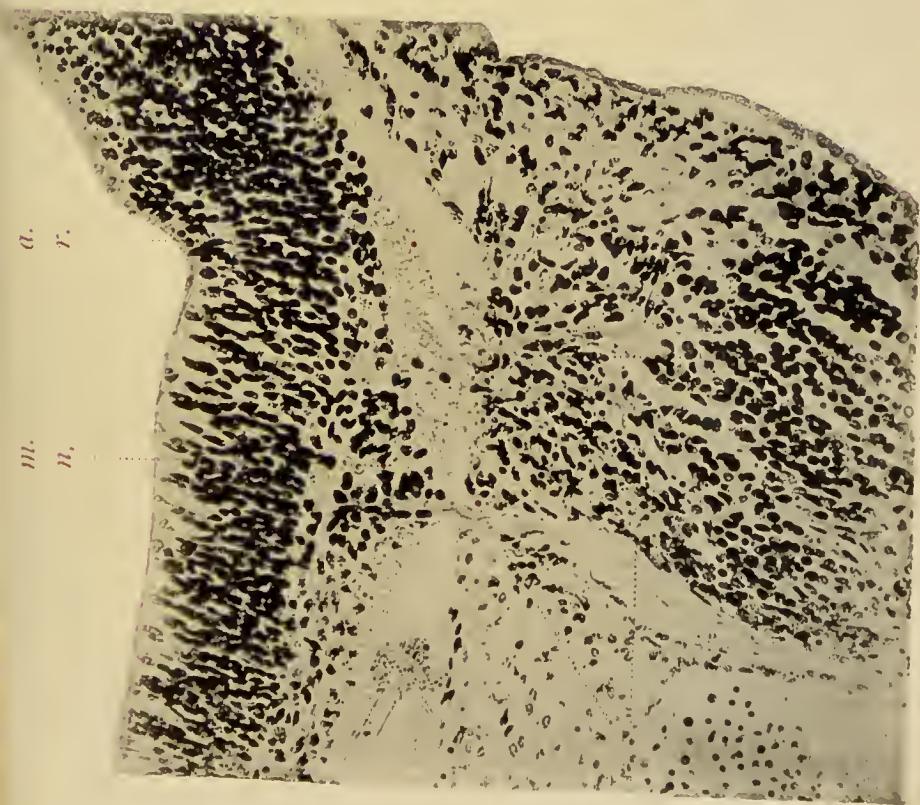
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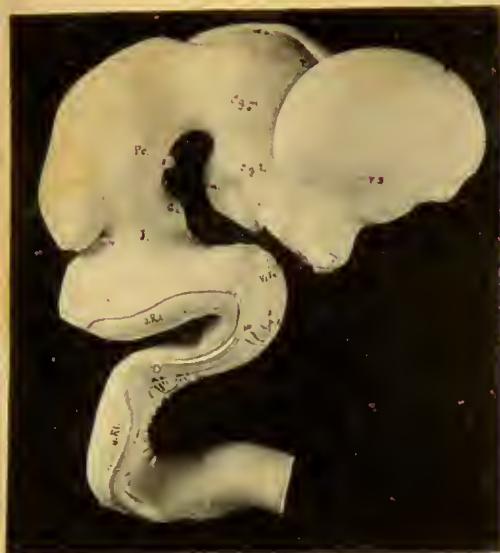
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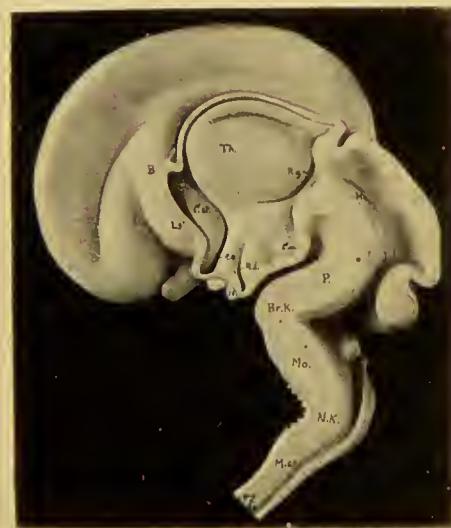
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w.   Wall of the brain-tube.

G.G.   Gasserian ganglion.

s.r.   Sensory root, formed of fibres growing out from the cells of the ganglion and entering the wall of the neural tube.

a.r.   The same fibres as represented by *s.r.* cut transversely owing to their having turned downwards to form the spinal root of the fifth nerve.

m.n.   Neuroblasts of the motor nucleus of the fifth nerve giving origin to the motor fibres —*m.r.*—which are seen growing out from the neural wall.

m.r.   Fibres of the motor root of the fifth nerve.

Human embryo of four weeks.